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ORIGINAL ARTICLE

Growth and longevity of *Mytilus edulis* (L.) from northeast Europe

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Abstract

The growth of mussels, *Mytilus edulis* (L.), was studied in most of the northeastern part of their distribution. The growth, longevity and maximal size of molluscs from 24 wild populations and one cultured population located in the White Sea and the southeast part of the Barents Sea were compared. The 25 studied populations were combined in six clusters. The maximal longevity and the size of the mussels varied between 7 and 18 years and 25.5 and 77.7 mm, respectively. The geographical location of the population within the studied region did not affect either maximal longevity or maximal size, or the growth rate of mussels. However, these parameters were influenced by local habitat conditions, primarily connected with the position within intertidal and subtidal zones. Animals inhabiting the intertidal zone were characterized by relatively low growth performance, a short life span and a small size. The longest life span was typical for deep subtidal mussels, whereas the highest growth rate was recorded in the cultured population and in the upper subtidal habitats. Growth patterns of *Mytilus edulis* in the subarctic White and the Arctic southeast Barents seas are similar to those reported from other parts of the area of distribution. Therefore, growth was mostly determined by local environmental factors, including those related to vertical zonation, rather than by latitude/longitude and related temperature effects.

Key words: Barents Sea, effect of habitat, growth, interpopulational and intrapopulational variation, longevity, maximal size, *Mytilus edulis*, White Sea

Introduction

Although it is widely considered that animals from colder environments grow slower, attain a larger size and live longer than their more warm-adapted conspecifics, the interpretation of data on growth and longevity of aquatic ectotherms in latitudinal gradients is controversial. Some species tend to increase longevity and maximal attainable size with increasing latitude (e.g. *Placopecten magellanicus*, MacDonald & Thompson 1988), whereas others demonstrate the opposite pattern (e.g. *Modiolus kurilensis*, Selin et al. 1991). In laboratory experiments on fish, in some cases significant growth compensation in cold-adapted animals was observed depending on nutritional conditions. When offered unlimited food resources, fish from higher latitudes outgrew their more southern conspecifics (Billerbeck et al. 2000; Yamahira & Conover 2002; Garvey & Marschall

2003). In other studies, animal growth was not compensated, indicating genetic differences between populations (Pörtner et al. 2001). Growth is considered to be an integral index of fitness of an organism and, therefore, is expected to decrease at the edges of a species' range (Hoffman & Parsons 1991; Hummel 2003). However, being a highly variable parameter, growth rate (including rate of gamete production) is modulated by numerous local exo- and endogenous factors that may conceal temperature effects. The degree of temperature compensation of growth in species distributed over different climatic zones remains unclear (see also Clarke 2003).

The mussel *Mytilus edulis* is a widely distributed bivalve mollusc in the North Atlantic inhabiting the European coastline from the Atlantic coast of France in the south to the Barents Sea and the western Kara Sea in the north. Therefore, it is a useful model for

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between-population comparisons (Zatsepin et al. 1948; Gosling 1992). Being a eurybiotic species, *M. edulis* can dominate in benthic communities in the regions with significantly different climatic regimes and occupy a broad variety of habitats, including intertidal and subtidal zones, estuaries, sheltered places and open rocky shores exposed to strong wave impact. In the White Sea, *M. edulis* is among the most abundant coastal invertebrates (see Lukanin 1985), whose diffuse and dense settlements form a belt in intertidal and upper subtidal zones. In the Barents Sea, and especially in the "Pechora Sea", which is the relatively shallow southeast part of the Barents Sea, mussel populations are poorly studied. It was generally considered that mussels were rare in the Pechora Sea (Zatsepin et al. 1948). In the 1990s, however, numerous productive benthic communities were described in the Pechora Sea (Denisenko et al. 2003). Mussel populations were found around Vajgach Island and near Khaypudyr Bay, where they served as nearly the sole food source for huge flocks of migrating waterfowl (our observations; Krasnov 2004). Due to their wide expansion and high ecological and commercial importance, *Mytilus* have been intensively studied for decades, often serving as a model for interpopulational comparisons (Bayne & Worrall 1980; Kautsky 1982; Munch-Petersen & Kristensen 2001; Sukhotin et al. 2006). Nevertheless, the growth of *M. edulis* in the northeast part of their range has not yet been studied. The present paper presents the first study of growth patterns in *M. edulis* in the White Sea and the southeastern part of the Barents Sea, with the aim of comparing the growth performance, maximal size and longevity of mussels from different populations.

Materials and methods

Environment

The climatic regimes of the White Sea and the Pechora Sea are similar. However, the latter is generally cooler. In the Pechora Sea, ice cover is formed annually, lasting for 8 months from October until June (Denisenko et al. 2003). In the south Pechora Sea, near the mainland, the surface water temperature reaches maximal values in August (mean +6–7°C) (Figure 1A). Salinity varies between 26 and 34‰, with a significant decrease in the estuaries. The climate at the White Sea has pronounced continental features with relatively warm summers and long severe winters (Berger & Naumov 2001). Ice covers the bays of the sea from December until May. Summer surface water temperatures show a gradient, with the highest values in Kandalaksha (Figure 1A), Onega and Dvina bays and decreasing temperatures

towards the north (Voronka, Mezen' Bay). The salinity of the surface waters varies between 24 and 27‰, falling down in the estuaries of big rivers. A seasonal decrease in salinity due to ice and snow melting in the spring is typical for both the White Sea and the Pechora Sea.

Material

Mytilus edulis (L.) were collected from 22 sites (stations) in the White Sea and the southeast part of the Barents Sea (Pechora Sea) during expeditions in July–August 1995, 1996 and 1997 (Figure 1B, Table I). Molluscs were sampled either by hand in the intertidal zone or using a Petersen grab (0.25 m²) in the subtidal zone. Samples from different habitats (e.g. intertidal, shallow and deep subtidal zones) within each location were treated separately. With the aim of recording the maximal age and animal size in different populations, the largest/oldest molluscs were targeted in the collection process. Although the sample size from Cape Russky Zavorot (RzUS) was very small due to significant logistical problems, this population was included in the analysis. Collected animals were dissected; shells were cleaned of epibionts and dried. The external structure of shells from all samples was examined. The age of mussels was determined by counting rings of winter growth delays on shells. The use of external growth rings on bivalve shells as a reliable estimate of a mollusc's age has been debated for the last three decades. It has been shown that in some species external rings do not reflect annual growth periodicity (Lutz 1976; Anwar et al. 1990), whereas in others annual growth delays (due to temperature extremes, food shortage or spawning) are clearly distinguishable (Theisen 1973; Brousseau 1984). The morphology of external growth rings and, therefore, their reliability in age determination shows latitudinal variability. *Mytilus* from the North Atlantic and Pacific show very distinct annual external growth marks (Andrews 1972; Theisen 1973; Zolotarev 1989), whereas in mussels from more temperate areas, the number of external rings and age are poorly correlated (Lutz 1976; Zolotarev 1989). Subarctic and Arctic regions studied in the present paper are characterized by highly pronounced seasonality with prolonged (5–6 months) periods of ice cover. These winter conditions of subzero temperatures combined with low primary production cause prolonged complete stops of mussel growth (Sirenko & Saranchova 1985; Sukhotin & Maximovich 1994) and make annual external winter marks clearly distinguishable from other (minor) rings caused by much shorter events (e.g. the low salinity period in the spring, spawning

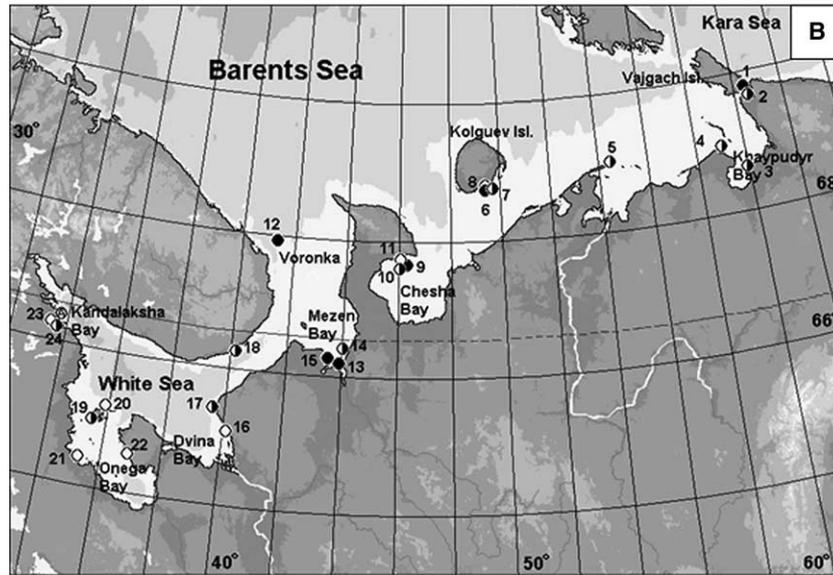
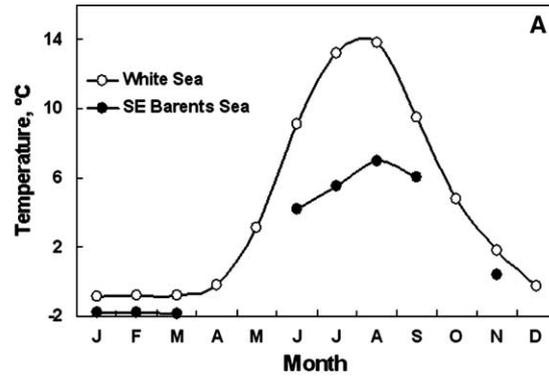


Figure 1. (A) Seasonal course of monthly mean surface water temperature in Kandalaksha Bay of the White Sea (Babkov 1982) and in the southeast part of the Barents Sea (Climatic Atlas of the Barents Sea 1998). (B) Map of the study area. Samples from deep (>5 m) subtidal, upper (<5 m) subtidal and intertidal zones are marked by black, half-filled and white circles, respectively. The location of aquaculture rafts is indicated by a circle with "A" inside.

in July and stormy weather in the autumn). The reliability of annual external rings as an age estimate has previously been verified in studies carried out in the White Sea by comparing the number of internal rings and seasonal growth of individually marked mussels of different ages and sizes (Chemodanov & Maximovich 1983; Sirenko & Saranchova 1985). The growth history of each mussel was reconstructed by measuring the maximal distance between the umbo and the most distant point of every winter mark on the shell. Data on mussel growth in Kandalaksha Bay of the White Sea (Keret' River estuary and Chupa Inlet) were taken from Sukhotin & Kulakowski (1992), where three habitats were represented: intertidal mussel bed (KeL), upper subtidal population (KeUS) and aquaculture population (CULT). In the latter habitat, molluscs were growing on 3 m ropes hanging from the rafts. Thus, we obtained six samples from the deep (>5 m) subtidal zone, 11 samples from the upper (<5 m)

subtidal zone, seven samples from the intertidal zone and one from aquaculture rafts.

Calculations and statistics

In all samples, growth for each mussel older than 4 years was reconstructed in accordance with individual growth history reflected in the shell external structure – winter marks. Growth curves were approximated using the von Bertalanffy growth equation

$$L_t = L_\infty \cdot (1 - \exp^{-k \cdot (t - t_0)}) \quad (1)$$

where L_t is the length (mm) at age t (years), L_∞ (asymptotic or theoretically maximal length, mm), k (rate at which L_∞ is approached, year⁻¹) and t_0 (theoretical time at which $L_t = 0$, year) are constants. Although individual growth curves of mussels in most cases were S-shaped with a small flexure at early years, we did not use the Gompertz model for growth description in order to compare our results with numerous literature data on mussels' growth

Table I. Location and brief description of sampling sites.

No.	Sea	Location	Coordinates	Sampling date	Habitat (zone, depth, exposure to waves, type of substrate)	Temperature (°C), salinity (‰)	Number of specimens	Symbol
1	Barents Sea	Yugorsky Shar Straits	69°45.507'N 60°33.319'E	28 July 1997	Subtidal 18 m; sheltered, gravel	2.5, 32	30	YuS
2	Barents Sea	Yugorsky Shar Straits	69°41.688'N 60°37.566'E	29 July 1997	Subtidal 1–3 m; sheltered, sand	6.2, 19	26	YuUS
3	Barents Sea	Khayndyr Bay	68°39.754'N 59°50.690'E	27 June 1995	Subtidal 1–3 m; sheltered, sand	6, 21.8	21	KhUS
4	Barents Sea	Cape Medynsky Zavorot	68°58.751'N 59°15.0'E	26 June 1995	Subtidal <5 m; open, sand	5.0, 29	35	MzUS
5	Barents Sea	Cape Russky Zavorot	68°59.189'N 54°37.736'E	25 June 1995	Subtidal <5 m; open, sand	7.0, 30	6	RzUS
6	Barents Sea	Kolguev Island	68°45.3'N 49°14.5'E	3 August 1997	Subtidal 6 m; sheltered, gravel, sand	6.7, 33	12	KoS
7	Barents Sea	Kolguev Island	68°46.350'N 49°15.539'E	2 August 1997	Subtidal 1–3 m; sheltered, sand	5.4, 33	19	KoUS
8	Barents Sea	Kolguev Island	68°46.350'N 49°15.539'E	2 August 1997	Intertidal; sheltered, big boulders	5.4, 33	10	KoL
9	Barents Sea	Chesha Bay	67°48.2'N 46°27.8'E	3 August 1997	Subtidal 16 m; sheltered, gravel	7.2, 34	19	ChS
10	Barents Sea	Chesha Bay	67°48.551'N 46°28.078'E	3 August 1997	Subtidal 1–3 m; sheltered, gravel	6.5, 34	19	ChUS
11	Barents Sea	Chesha Bay	67°48.551'N 46°28.078'E	3 August 1997	Intertidal; sheltered, rocks	6.5, 34	10	ChL
12	White Sea	Voronka	67°54.420'N 41°23.250'E	5 August 1997	Subtidal 37 m; open, gravel	8.0, 32	30	VoS
13	White Sea	Mezen Bay, Mezen Estuary	66°13.012'N 43°39.417'E	22 June 1995	Subtidal 10 m; open, sand	9.0, 25	10	MeS
14	White Sea	Mezen Bay, Mezen Estuary	66°39.781'N 44°05.607'E	23 June 1995	Subtidal <1 m; sheltered, rocks	8.0, 27	28	MeU
15	White Sea	Mezen Bay, Kuloy Estuary	66°12.254'N 43°40.932'E	23 June 1995	Subtidal 10 m; sheltered, sand	10.5, 25	12	KuS
16	White Sea	Dwina Bay	65°05.600'N 40°04.750'E	5 July 1995	Intertidal; sheltered, sand	17.0, 19	17	DwL
17	White Sea	Dwina Bay, Kozly	65°15.532'N 39°52.383'E	6 August 1997	Subtidal <1 m; open, gravel, boulders	16.3, 22	25	DwUS
18	White Sea	Tersky Shore, Pulonga	66°15.465'N 40°00.909'E	5 August 1997	Subtidal <1 m; open, sand	8.9, 28	24	TeUS
19	White Sea	Solovetsky Island	65°02.141'N 35°40.624'E	8 August 1997	Subtidal <1 m; sheltered, boulders	18.0, 26	20	SoUS
20	White Sea	Anzer Island	65°08.577'N 35°56.127'E	9 August 1997	Intertidal; open, gravel	10.3, 27	15	AnL
21	White Sea	Onega Bay, Kuzov	64°55.126'N 35°15.0'E	8 August 1996	Intertidal; sheltered, rocks	16.0, 26	35	KuzL
22	White Sea	Onega Bay, Konukhova	64°54.0'N 36°40.0'E	8 August 1996	Intertidal; sheltered, boulders	16.2, 26	39	KonL
23	White Sea	Kandalaksha Bay, Keret' Estuary	66°18.888'N 33°47.119'E		Intertidal; sheltered, gravel		50	KeL
24	White Sea	Kandalaksha Bay, Keret' Estuary	66°18.888'N 33°47.119'E		Subtidal 2 m; sheltered, gravel		50	KeUS
25	White Sea	Chupa Inlet	66°20.230'N 33°38.972'E		Aquaculture; sheltered		72	CULT

usually approximated by a von Bertalanffy model. Because mussels younger than 4 years old in studied populations have not shown growth deceleration yet, their growth could not be described by the von Bertalanffy model. Thus, they were excluded from the analysis.

A comparison of mussel growth in the studied sites was performed using two estimates: (1) overall growth performance index (OGP), proportional to the maximal rate of size increase during the lifetime, was calculated as $OGP = \log(L_{\infty} \times k)$ (Pauly 1979, cited in Brey 2001); (2) a pairwise comparison of growth curves and their clustering was performed according to an algorithm suggested by Maximovich (1989). Briefly, the significance of the differences between growth curves was determined using the ratio of the residual variances $F = S_I^2/S_{II}^2$. S_I^2 was calculated for each of the compared growth curves as $S_I^2 = (SS_1 + SS_2)/(n_1 - 3 + n_2 - 3)$, where SS_1 and SS_2 are the sums of squares of variants' deviations from the separate compared regression lines 1 and 2; n_1 and n_2 are the numbers of variants in each of the compared lines. S_{II}^2 was calculated as $S_{II}^2 = SS/(n_1 + n_2 - 3)$, where SS is the sum of squares of variants' deviations from the common regression line based on the pooled data. The ratio of Fisher's F-statistic to the critical F value at $P < 0.05$, F/F_{cr} , was used as a measure of distance between the compared curves. The value of $F/F_{cr} < 1$ meant the absence of significant differences between the compared growth lines. Clustering was performed using a method of weighed pairgroup average. The integration of the growth curves was carried out starting with the pair characterized by the lowest value of F/F_{cr} ratio.

Growth curves of all individual mussels were compared within each sample. Eleven samples (YuS, KoUS, ChS, ChUS, TeUS, DwUS, SoUS, KhUS, DwL, KuzL, KonL) contained mussels significantly differing ($P < 0.05$) in growth curves, which resulted in separate clusters within each sample (data not shown). Within each of these samples, the cluster, which combined mussels showing the highest growth rates (fast-growing mussels), was defined and treated separately. Thus, for each population (sample), growth curves were obtained describing the average growth of all mussels and only the fast-growing ones. In populations without significant growth heterogeneity, the average growth rate was also the highest one; therefore, all mussels were assumed to be fast growing. Thus, the growth equations for all mussels and fast-growing mussels coincided for such populations.

Absolute annual growth increments of mussels (ΔL , mm year⁻¹) were calculated as

$$\Delta L = L_{t+1} - L_t$$

where L_t and L_{t+1} (mm) are the length of the mussel at the age of t and $t+1$ years, respectively, determined by winter marks on the shell.

The oldest and the largest animal encountered in a sample represented the maximal age and size attained by mussels in the population. The accuracy of maximal longevity and maximal size estimation in the population obviously depends on the sample size or the duration of the study period (Beukema 1989). For maximal size and age estimation we collected the largest and the oldest animals from each population, which were usually not abundant (see Table I). At some stations the population size was extremely small (MeS, KuS), whereas in other places the populations were mostly represented by small molluscs, younger than 4 years old (KoL, ChL). Although this may potentially lead to an underestimation of the maximum longevity and size, we assumed that the error of estimation was similar among different populations and, therefore, the present data adequately reflect the main trends.

Kruskal–Wallis rank ANOVA was used for analysing the effects of the factor habitat (intertidal, upper subtidal, low subtidal) and sea (Barents Sea and White Sea) on mussel longevity, maximal size and OGP values. A regression analysis was performed to relate these parameters to depth in subtidal habitats, latitude and longitude. If not specially noted then mean values \pm standard error are presented.

Results

Maximal life span and size

Under aquaculture conditions, the maximal age and size of mussels depend on the cultivation technology and are restricted by the cultivation cycle. Molluscs are harvested before they reach their maximal age and size and consequently the observed values do not reflect natural abilities of mussels to survive in this specific habitat. Therefore, the sample of mussels from the aquaculture rafts (CULT) was excluded from the analysis of longevity and maximal size. The maximal life span in other studied populations varied from 7 to 18 years (Table II). The oldest specimens were recorded in the deep subtidal population from the most northeast station – Yugorsky Shar straits connecting the Barents Sea and the Kara Sea. Three intertidal populations from both the White and the Barents seas were characterized by the lowest maximal life span of mussels – 7 years old. Vertical zonation was the main factor significantly influencing this parameter (ANOVA, $P < 0.05$). In general, mussels lived longer in subtidal > 5 m depth, whereas the shortest life span was observed in intertidal populations (Figure 2). Within the subtidal zone, depth was

Table II. Growth parameters of mussels.

No.	Site	Maximum age (years)	Maximum length (mm)	All mussels				Fast-growing mussels			
				L_{∞} (mm)	k (year ⁻¹)	t_0 (year)	OGP	L_{∞} (mm)	k (year ⁻¹)	t_0 (year)	OGP
1	YuS	18	64.8	119.1	0.044	1.27	0.72	87.5	0.098	2.124	0.93
2	YuUS	9	59.4	250.8	0.027	1.217	0.84				
3	KhUS	13	50.5	98.7	0.095	0.759	0.97	158.8	0.064	0.755	1.01
4	MzUS	12	70.0	115.6	0.080	1.492	1.05				
5	RzUS	11	75.2	81.6	0.153	1.482	1.10				
6	KoS	14	63.0	111.1	0.070	1.553	0.89				
7	KoUS	13	74.9	193.0	0.037	1.416	0.85	118.7	0.097	1.685	1.06
8	KoL	7	44.5	73.5	0.155	1.751	0.97				
9	ChS	15	77.0	77.9	0.157	1.736	1.18	99.8	0.152	1.651	1.18
10	ChUS	15	72.8	75.9	0.170	1.506	1.16	78.9	0.183	2.162	1.16
11	ChL	8	36.4	163.5	0.035	0.739	0.76				
12	VoS	13	71.7	133.4	0.068	0.973	0.96				
13	MeS	10	56.6	191.8	0.042	1.521	0.85				
14	MeUS	10	66.4	90.5	0.126	1.443	1.03				
15	KuS	11	48.8	66.9	0.124	0.713	0.92				
16	DwL	14	49.8	71.2	0.096	0.578	0.83	113.5	0.071	0.864	0.91
17	DwUS	11	56.2	138.0	0.048	0.701	0.82	106.8	0.090	0.845	0.98
18	TeUS	9	54.0	100.5	0.095	1.026	0.98	101.4	0.101	0.986	1.01
19	SoUS	12	77.7	85.8	0.153	0.677	1.12	121.6	0.128	0.758	1.19
20	AnL	7	25.5	27.7	0.263	1.025	0.67				
21	KuzL	12	41.8	75.9	0.075	0.808	0.76	56.9	0.227	1.456	1.11
22	KonL	9	45.5	82.8	0.084	0.828	0.84	132.5	0.068	0.970	0.96
23	KeL	7	45.0	54.8	0.116	0.293	0.80				
24	KeUS	10	64.0	77.1	0.140	0.611	1.03				
25	CULT	10	84.1	92.9	0.196	0.741	1.26				

L_{∞} , k, t_0 , parameters of the von Bertalanffy growth equation; OGP, overall growth performance index; OGP = $\text{Log}(L_{\infty} \times k)$.

not a significant factor modulating maximal life span (regression analysis, $R^2 = 0.183$, $P > 0.05$). Neither latitudinal nor longitudinal variation affected the maximal life span of mussels. On average, the Barents Sea populations were characterized by maximal longevity of 12.3 years, whereas in the White Sea it reached 10.4 years. However, the difference was insignificant (ANOVA, $P > 0.05$).

The maximal age of mussels was positively correlated with the maximal reached size (Spearman $R = 0.601$, $P < 0.01$, $n = 24$). The maximal size reached by mussels varied by more than three-fold, from 25.5 mm in intertidal populations on Anzer Island (AnL) to 77.7 mm recorded in the upper subtidal from Bolshoy Solovetsky Island (SoUS). Basically, intertidal populations were characterized by smaller sized mussels (ANOVA, $P < 0.001$), whereas molluscs in the upper and deep subtidal zones reached similar maximal size (Figure 2). Factors "latitude", "longitude" and "sea" did not significantly influence the maximal size of mussels.

Growth variation

The parameters of von Bertalanffy equations describing mussel growth are presented in Table II. We assumed that only fast-growing mussels in each

population realized the maximal potential for growth of the species within the resources available in a specific site/habitat (Savilov 1953; Gogolev & Selin 1987; Vuorinen et al. 2002). Therefore, populations were compared using only growth equations of fast-growing specimens. A statistical comparison and a clustering procedure of the obtained growth curves of the fast-growing mussels showed that 25 investigated populations could be divided into six clusters with significantly ($P < 0.05$) different growth equations (Table III, Figure 3A, B). Cluster I included populations with the most rapid growth of mussels (OGP = 1.26) – the suspended culture (CULT) and the upper subtidal population at Bolshoy Solovetsky Island (SoUS). By the age of 4 years old, mussels in these populations could attain a size of approximately 45 mm. The annual absolute growth increments (ΔL) of fast-growing mussels from these two populations reached more than 14 mm at the fourth year and rapidly decreased thereafter (Figure 3C). Each of clusters II and V was represented by the only deep subtidal population – from Chesha Bay (Barents Sea) and from Kuloy River estuary (White Sea), respectively (Table III, Figure 3A, B). These two populations demonstrated the range of growth variation within the deep subtidal habitat. Mussels from Chesha Bay grew faster than those from Kuloy

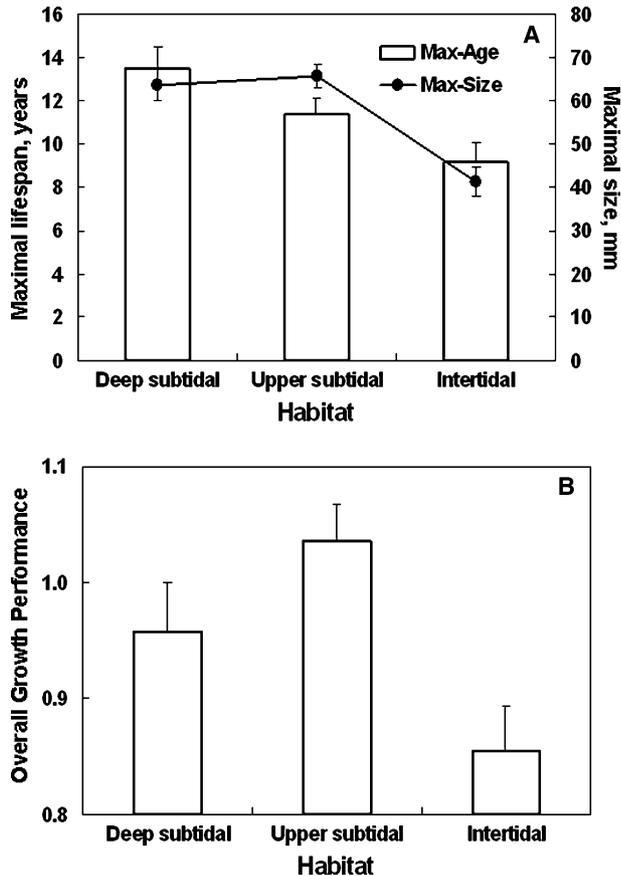


Figure 2. Maximal size, longevity (A) and overall growth performance (B) of mussels from intertidal and subtidal zones. Error bars represent standard errors.

estuary, and attained a larger size and longevity (Table II). ΔL values were also significantly higher in the cluster II mussel population than in cluster V, although showing a similar age-dependent pattern with a maximum at 4 years of age (Figure 3C). The absolute majority of the studied populations (19 from 25) fell into two intermediate clusters (clusters III and IV, OGP=1.01 and 0.85, respectively). Cluster III combined mostly upper subtidal popula-

tions from both the Barents and the White seas. The deepest subtidal population (37 m) from Voronka, as well as several intertidal settlements, including the most northern one (KoL), were also in this group. Annual length increments in these populations were maximal during the fourth and fifth years, and after the seventh year they stabilized at the values between 4 and 6 mm year⁻¹ (Figure 3C). Populations combined in cluster IV were characterized by a relatively low growth rate of mussels, with ΔL values varying around 6 mm year⁻¹ from 3 to 10 years of age and about 2 mm year⁻¹ thereafter. Both samples from Yugorsky Shar straits (YuS and YuUS) were combined in cluster IV with two deep subtidal and one intertidal population. The most long lived animals from KoS and YuS were represented in cluster IV. The lowest growth rate was characteristic for mussels comprising the last cluster VI (Figure 3A). This group consisted of the two intertidal White Sea populations from Keret' estuary (KeL) and from Anzer Island (AnL). In these locations, mussels typically did not reach 30 mm in length by the highest recorded age – 8 years old (Figure 3B). Three-, 4- and 5-year-old specimens were characterized by the most active growth, with similar annual increments of approximately 5 mm. A gradual decrease in ΔL values was recorded after 5 years of age (Figure 3C).

Overall, growth performance among the fast-growing mussels was significantly dependent on vertical zonation (Kruskal–Wallis ANOVA, $P < 0.01$), with the lowest values observed in intertidal habitats and the highest in upper subtidal habitats (Figure 2).

Discussion

Bivalves include the most long-lived mollusc species (for a review see Heller 1990), whereas *Mytilus* species are characterized by intermediate longevity (Golikov 1985; Zolotarev 1989). The oldest

Table III. Clustering of growth curves of fast-growing mussels.

Cluster no	Populations included	Fast-growing mussels			
		L_{∞} (mm)	k (year ⁻¹)	t_0 (year)	OGP
I	CULT, SoUS	95.3	0.189	0.800	1.26
II	ChS	99.8	0.152	1.651	1.18
III	MzUS, RzUS, KhUS, KoUS, KoL, ChUS, MeUS, DwUS, KeUS, TeUS, DwL, VoS, KuzL, KonL	112.4	0.090	1.343	1.01
IV	YuUS, YuS, KoS, MeS, ChL	115.2	0.062	1.285	0.85
V	KuS	66.9	0.124	0.713	0.92
VI	AnL, KeL	85.6	0.060	0.897	0.71

L_{∞} , k , t_0 , parameters of the von Bertalanffy growth equation; OGP, overall growth performance index; $OGP = \text{Log}(L_{\infty} \times k)$.

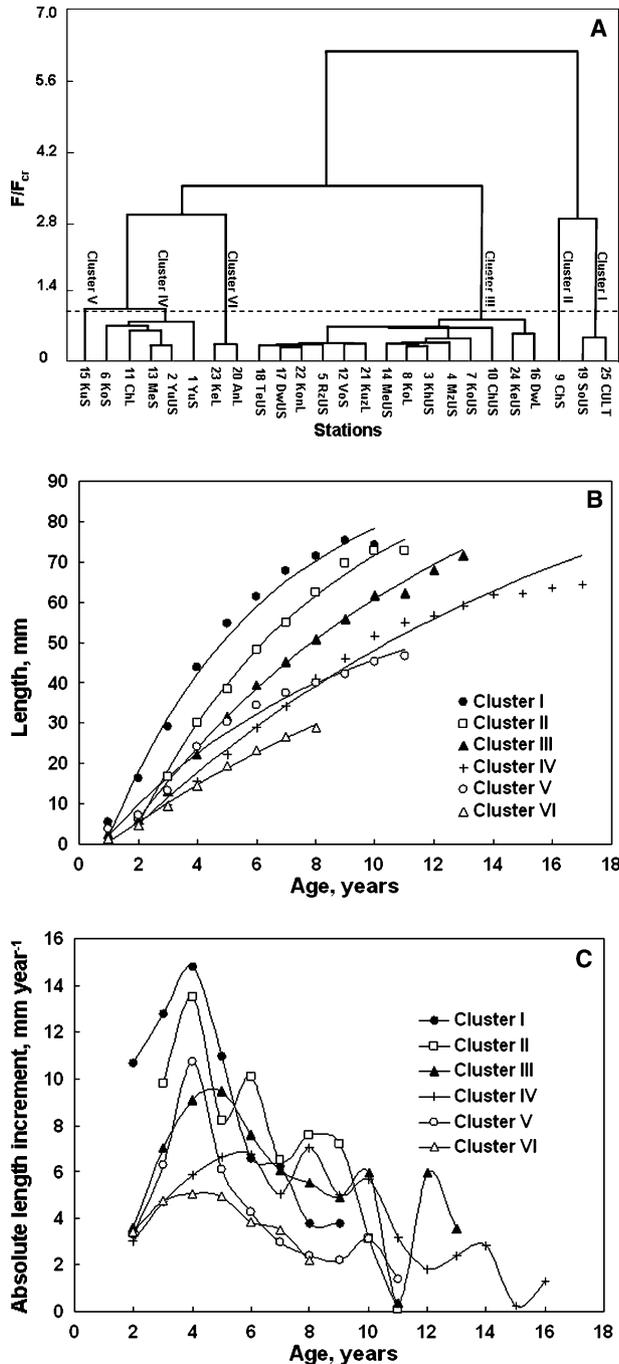


Figure 3. Clustering of the studied populations by growth curves of the fast-growing mussels (A). Y-axis, F/F_{cr} ratio as a measure of the distance between compared curves (see text). The dotted line shows $F/F_{cr} = 1$, below which the difference of compared curves was not significant at $P < 0.05$. (B) Growth curves of fast-growing mussels from populations combined in six clusters (see text). (C) Annual growth increments of fast-growing mussels from populations combined in six clusters (see text).

M. edulis specimens are reported from the Kandalaksha Bay of the White Sea (25 years old; Savilov 1953) and from the western coast of Greenland near Thule (24 years old; Theisen 1973). In the present study, the maximal longevity of mussels ranged from

7 to 18 years and, thus, was within the known limits. The maximal size and age of molluscs were lowest in the intertidal zone (Figure 2), which corresponds with previous observations (Savilov 1953; Baird 1966; Maximovich 1989).

The lowest values of maximal size and longevity observed in the two intertidal populations (AnL and KeL) may be caused by different factors. Mussel settlement at Anzer Island is situated on an open shore. It is exposed to the winds of west, north and east directions and, therefore, to a strong wave action. The life span and size of mussels in the intertidal zone may be limited by mechanical factors, such as extreme wave or, in high latitudes, abrasive ice action. On exposed shores, mussels usually inhabit narrow crevices in the rocks or boulders where they are protected from detachment by waves and ice. The maximal size in such a habitat is restricted by the available space because animals sticking out from crevices are mechanically removed. Lower longevity of animals from exposed shores compared with that of mussels from sheltered habitats has been reported for *Perna perna* (McQuaid & Lindsay 2000), *M. galloprovincialis* (Steffani & Branch 2003) and *M. edulis* (Savilov 1953; Sukhotin et al. 2006). The KeL and KeUS samples were taken from tidal and upper subtidal parts of one population located in the estuary of the Keret' River. The place is washed by strong tidal currents and is characterized by low salinity, caused by river run-off distributed mainly in the upper water layer, where salinity may decrease to 10‰ (Basova et al. 2004). In contrast to the intertidal ones, upper subtidal mussels (KeUS) were not subjected to air exposure and possible effects of low salinity, but benefited from extensive hydrodynamic mixing and thus showed a relatively high growth rate.

Growth performance values were also lower in intertidal habitats than in subtidal ones. This is typical for mussels (Baird 1966; Seed 1969; Sukhotin & Maximovich 1994) and other bivalves (Bertness & Grosholz 1985; Franz 1993 and many others). However, among the studied intertidal populations, growth varied significantly, which was reflected in the fact that intertidal settlements were represented in different (III, IV and VI) clusters (Table III). The OGP of fast-growing intertidal mussels (mean value 0.85) ranged between 0.76 in Chesha Bay of the Barents Sea (ChL) and 1.11 in Onega Bay of the White Sea (KuzL) (Figure 2). It is notable that a similar OGP can be calculated from growth data reported for significantly latitudinally separated intertidal populations. Thus, OGP values were 1.09 for *M. edulis* from Helgoland Island (North Sea, approximately 54°N) (Sukhotin et al. 2006) and 1.08 for

mussels from Disko Bay in western Greenland (at approximately 69°N) (Theisen 1973).

The maximal size attained by subtidal mussels varied among populations in a wide range from approximately 50 mm (KuS and KhUS) to nearly 80 mm (ChS and SoUS) and did not significantly differ between deep and upper subtidal habitats (Figure 2). In general, upper subtidal animals grew faster and possessed lower values of maximal longevity than those from deep subtidal populations (OGP = 1.04 and 0.96, respectively). The absolute majority of upper subtidal populations were combined in the intermediate cluster III with an average OGP of 1.01 (Table III). The two exceptions were: YuUS and SoUS populations, characterized by the slowest and the most rapid mussel growth among the upper subtidal populations, respectively. The population in the Yugorsky Shar Straits (YuUS) was the most distant northeast outpost of *M. edulis* within the studied region, situated at the eastern border of the area of distribution. The nearest findings of *M. edulis* at this or higher longitudes were recorded at the southwest coast of Novaja Zemlia Archipelago up to Matochkin Shar Straits to the north (approximately 73°N) and along the western coast of Bajdaratskaya Bay of the Kara Sea (approximately 65°E) (Zatsepin et al. 1948). It is probable that either mussels experience food scarcity in that area because of a very short phytoplankton growth period or growth is impeded by extremely low temperatures (Table I). The population at Bolshoy Solovetsky Island (SoUS) lay 0.5 m deep, where mussels covered large boulders in the basis of an old dyke built in the seventeenth century. The dyke delimited a small shallow bay called Filippovskie Sadki (Phillip Cages) from the sea, causing constant strong water movements due to tidal currents. Thus, the mussel population was situated in a relatively warm surface water layer in the place with extensive water movements, which probably allowed a very rapid growth of mussels comparable with that observed in the most favourable conditions of suspended aquaculture (CULT).

Although “deep subtidal” populations were located in a wide range of depths (from 6 to 37 m), depth was not a significant factor influencing the growth rate or maximal attainable size of mussels. This finding corresponds to other observations on *Mytilus* (Richardson et al. 1990; Antsulevich et al. 1999). Animals from the deepest studied site in the Voronka region of the White Sea (VoS, 37 m) reached a length of 50 mm in 7 years, which was faster than in the majority of the deep and even upper subtidal populations. This may be due to the very high hydrodynamics in the region. Tidal currents in the Gorlo Straits and the Voronka part

of the White Sea are turbulent and intensively mix the water body, reaching velocities of up to 250 cm s⁻¹ (Berger & Naumov 2001). Among deep subtidal populations, the maximal growth performance (OGP = 1.16) was characteristic for Chesha Bay of the Barents Sea, whereas the lowest OGP of 0.92 was recorded in a population from the Kuloy River estuary. The bottom of Chesha Bay is covered with mussels with an average biomass of the population of 147 g wet weight m⁻², and with individuals reaching a size of 6–8 cm (Guryanova 1925). These findings indicate that environmental conditions in the subtidal zone of Chesha Bay are favourable for mussels. However, we lack precise hydrological data for this area. The Kuloy River, unlike Mezen', carries much sand and other particles, which makes the water very turbid (our visual observations). We suggest that the growth of mussels in the Kuloy Estuary may be affected by high turbidity combined with a low organic value of the particulate matter. However, a single sample studied from this habitat does not permit generalizations.

The maximal size of *M. edulis* in wild populations did not exceed 80 mm, which is typical for this species, although mussels of larger sizes (up to 100 mm) rarely occur in subtidal habitats, even in the studied region (e.g. in the SoUS population, V. M. Khaitov, pers. commun.). Aquaculture conditions usually include placing of a seed in the most nutrient-rich water layers and application of special measures preventing intraspecific competition (for a review see Gosling 2003). This increases food availability, thereby enhancing the growth of molluscs and raising the upper limit of attainable size. *Mytilus edulis* in cultured populations frequently reach sizes over 80 mm. Provided with unlimited time, most of the mussels under suspended aquaculture conditions in the White Sea die at about 10 years of age (Maximovich & Sukhotin 2005). However, in rare cases, 16-year-old individuals have been encountered (B. L. Kunin, pers. commun.).

Mytilus edulis in the studied part of their distribution demonstrated almost the whole spectrum of growth performance recorded for the species (Figure 4). Growth patterns of mussels from the most northern *Mytilus* populations from western Greenland (Theisen 1973) are similar to those found in molluscs combined in clusters III–VI of the present study. Animals can reach approximately 70 mm (over 90 mm in exceptional cases; Theisen 1973) over a period of 10 to more than 20 years, depending on habitat. In temperate areas, mussels usually grow faster than in higher latitudes, but only at young ages. Thus, mussels from the North Sea exceeded in size the animals from cluster I during the first 2–4 years, whereas afterwards their growth was similar to that of

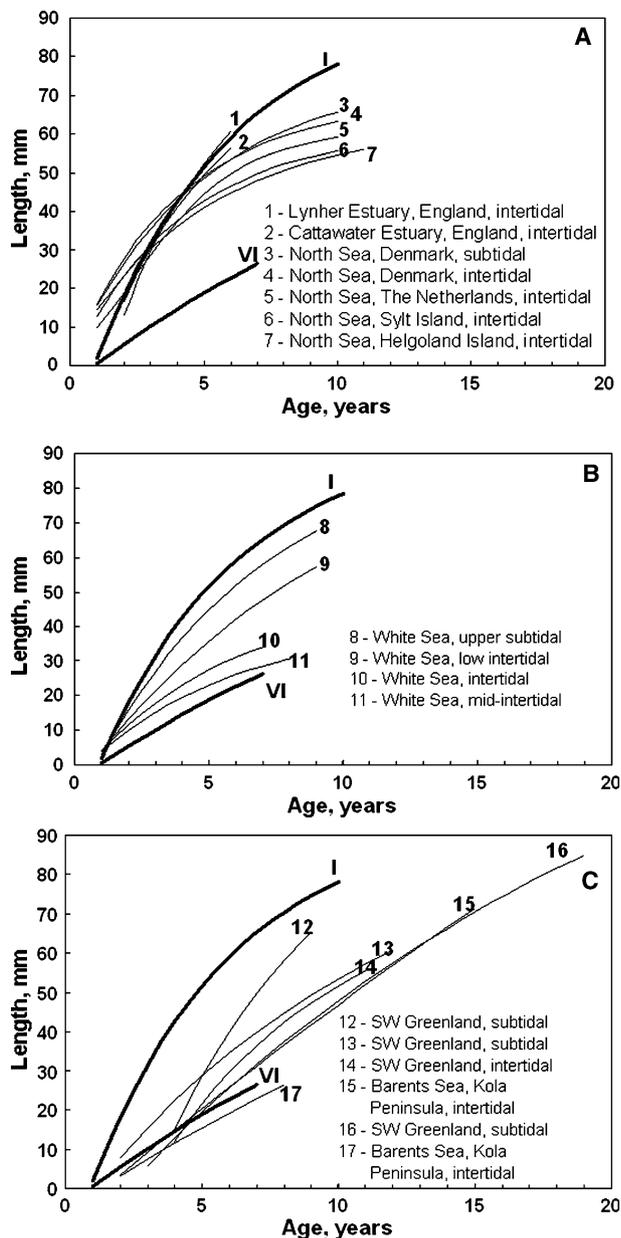


Figure 4. Growth curves of *Mytilus edulis* from different regions of the North Atlantic: (A) temperate seas, (B) subarctic White Sea, (C) Arctic Barents Sea and Greenland. The range of growth variation is represented by clusters I and VI from the present study. 1- $L_{\infty}=93.8$, $k=0.222$, $t_0=1.32$ (Bayne & Worrall 1980); 2- $L_{\infty}=81.3$, $k=0.237$, $t_0=1.04$ (Bayne & Worrall 1980); 3- $L_{\infty}=75.8$, $k=0.198$, $t_0=-0.16$ (Munch-Petersen & Kristensen 2001); 4- $L_{\infty}=69.3$, $k=0.243$, $t_0=-0.08$ (Munch-Petersen & Kristensen 2001); 5- $Lt=61.37 \times e^{(-2.8 \times \exp(-0.431t))}$ (Craeymeersch et al. 1986); 6- $L_{\infty}=61.5$, $k=0.236$ (Asmus 1987); 7- $L_{\infty}=62.8$, $k=0.197$, $t_0=-0.34$ (Sukhotin et al. 2006); 8- $L_{\infty}=95.5$, $k=0.150$, $t_0=0.78$ (Maximovich 1989); 9- $L_{\infty}=79.0$, $k=0.076$, $t_0=0.63$ (Maximovich 1989); 10- $L_{\infty}=49.1$, $k=0.183$, $t_0=0.52$ (Maximovich 1989); 11- $L_{\infty}=41.8$, $k=0.175$, $t_0=0.42$ (Maximovich 1989); 12- $L_{\infty}=105.6$, $k=0.162$, $t_0=3.07$ (Theisen 1973); 13- $L_{\infty}=98.5$, $k=0.087$, $t_0=1.04$ (Theisen 1973); 14- $L_{\infty}=77.5$, $k=0.155$, $t_0=2.91$ (Theisen 1973); 15- $L_{\infty}=412$, $k=0.014$, $t_0=1.38$ (Sukhotin et al. 2006); 16- $L_{\infty}=153.3$, $k=0.048$, $t_0=2.19$ (Theisen 1973); 17- $L_{\infty}=126.2$, $k=0.035$, $t_0=1.26$ (Sukhotin et al. 2006).

mussels from clusters II and III (Craeymeersch et al. 1986; Asmus 1987; Munch-Petersen & Kristensen 2001; Sukhotin et al. 2006). Molluscs from two low intertidal populations in southern England demonstrated similar growth pattern as mussels from the SoUS site, reaching approximately 60 mm by 6 years of age (Bayne & Worrall 1980). However, no data are available on the growth of older specimens there and whether they exist. Moreover, mussel populations studied by Bayne & Worrall (1980) probably contained *M. galloprovincialis* or hybrids of *M. galloprovincialis* and *M. edulis*, rather than *M. edulis* (Gosling 1992). Thus, although in general molluscs from southern parts of their distribution reach maximal size somewhat earlier than their northern conspecifics, the latter ones maintain relatively intensive growth in the advanced ages. This may be due to possibly different patterns of assimilated energy allocation to gametogenesis in the lifetime course along geographical clines. Because aquatic ectotherms in northern populations have lower fecundity than those in the south (MacDonald & Thompson 1988; Pörtner et al. 2001), the relative proportion of somatic growth may well be kept constant for a longer time at high latitudes (see also Clarke 1987).

Numerous within-species comparisons of molluscan growth in geographically distant populations gave contradictory results. Thus, in some studies, geographical, mostly temperature-determined differences in growth rate and/or maximal attainable size of animals were observed (*Macoma balthica*, Gilbert 1973; *Modiolus difficilis*, Gogolev & Selin 1987; *Modiolus kurilensis*, Selin et al. 1991). Others stated that latitudinal (temperature) effects on growth were compensated (polychaete *Ophryotrocha puerilis*, Levinton & Monahan 1983; fishes *Menidia* sp., Yamahira & Conover 2002; *Micropterus salmoides*, Garvey & Marschall 2003; see also for molluscs: Golikov 1975) or may be overruled by other environmental factors making geographical and local growth variation similar (*Mytilus edulis*, Jørgensen 1990; *Arctica islandica*, Witbaard et al. 1999). In the present study, geographical distribution did not significantly influence any of the studied parameters – maximal size, life span and overall growth performance – in mussels from the studied populations. On the contrary, vertical distribution significantly affected the growth rate, size and longevity of mussels. Intertidal populations showed the lowest values of all these parameters. The growth rate in deep subtidal habitats was somewhat higher, but maximal size was significantly higher than in intertidal populations. The maximal attainable size in upper and deep subtidal zones was similar, but growth rate (the rate at which this size is reached) was higher in the upper subtidal zone, which

determined the intermediate values of longevity (Figure 2).

In continuously growing animals, the maximal life span, maximal size and growth rate are functionally interrelated (see also Jørgensen 1976; Hawkins & Bayne 1992; Charnov et al. 2001). Maximal size is determined by morphological constraints of an organism and also by environmental parameters, which restrict the animal's size to a certain limit, either mechanically (e.g. wave or ice action, predation) or by setting an upper boundary of energy supply due to either external (food availability or stress factors increasing an energetic "cost" of life, e.g. low salinity) or internal (e.g. physiological limitations of energy acquisition) factors, or both. Maximal longevity depends on the maximal size, which can be attained by the species in a certain habitat, and on the growth rate, at which this maximal size is approached. Growth rate is also an extremely variable parameter. Similar to the maximal size, it is modulated in bivalves by a complex combination of biotic or abiotic environmental factors (for reviews see Seed & Suchanek 1992; Gosling 2003) and endogenous influences, such as genotype, physiological status, or energy partitioning between somatic growth and reproduction (for a review see Hawkins & Bayne 1992). Our data suggest that growth patterns of *M. edulis* in the subarctic White and the Arctic Barents seas are similar to those reported from other parts of the area of distribution. Even at the northern limits of their distribution (Zatsepin et al. 1948; Gosling 1992), mussels demonstrate a wide variety of growth rates, maximal longevity and attainable size within and between separate populations, which is comparable with the range observed over the whole latitudinal distribution range of this species. Therefore, growth is mostly determined by local environmental factors (e.g. salinity, hydrodynamics and food supply) rather than by latitudinal or longitudinal and related temperature effects.

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